
RESEARCH ARTICLES

SIZE AND MATING SUCCESS IN A NON-TERRITORIAL DAMSELFLY *XANTHAGRION ERYTHRONEURUM* (ZYGOPTERA: COENAGRIONIDAE)

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(Received February 14, 1997)

ABSTRACT

Flight activity and reproductive behaviour of the damselfly *Xanthagrion erythroneurum* (Zygoptera: Coenagrionidae) was observed over a 2 year period (1989-1990). Marked insects were censused hourly between 0900 - 1600 hs each day for 6 weeks in each year where, in addition to presence or absence, records were made of individual behaviour including mating and oviposition. Evidence for male-male behaviour was tested using models of both sexes. All observations and experiments were conducted at a focal pond close to Perth, Western Australia.

Sex ratios of damselflies visiting the pond were male biased; males tended to arrive at the pond ahead of females. Sexual maturity, as indicated by the first attempts to mate were measured for both sexes. Both sexes matured within 8 days from emergence. Daily survival rate was estimated by the number of times individuals returned to the focal pond. Conservative estimates of survival were 80% for males and 70% for females.

Males showed no signs of agonistic behaviour either towards other flying or perched males or towards the models of either sex. *X. erythroneurum* showed no signs of territorial behaviour.

Mating behaviour involved males intercepting perched or flying females. Pairs adopted the tandem and wheel positions typical of all odonates. Oviposition immediately followed mating. Males remained with the submerged females or on the surface of the water close to the submerged female. Females remained underwater for an average of 35 mins. On emergence other males attempted to copulate with the female, adopting the tandem position for several minutes. No successful copulations were observed and males released the previously mated female within minutes.

Although age had a significant effect on mating success, size (head width and wing length) of adult males and females had no effect on mating success. Both males and females close to 7 days post-emergence had the greatest chance of mating.

INTRODUCTION

Mating in animals is often not random, and may be controlled by attributes of either sex¹. Assortative mating by size is one of the more common patterns of mating in natural populations^{2,4} and assumes that larger individuals either hold more valuable resources, in the case of males, or are more fecund in the case of females⁵⁻⁶. Not surprisingly many studies show that large males obtain more mates than small males but over an individual's lifetime

differences in fitness between small and large animals may not be significant, or may even be reversed⁷.

The effects of body size on mating success within the Odonata have been subject to short- and long-term studies. For example, in a short-term study, Harvey and Corbet⁸ found that in *Pyrrosoma nymphula* large males win more territorial disputes and obtain more mates than small males. Similar results were found by Tsubaki and Ono⁹ for *Nannophya pygmaea*. On the other hand, studies of lifetime mating success of the non-territorial damselflies, *Coenagrion puella*¹⁰ and *Enallagma hageni*¹¹, revealed that intermediate-sized males were more likely to mate than the larger males. There are two issues here. First, short-term studies may provide an inaccurate estimate of fitness differences and second, body size may be of greater importance in territorial rather than in non-territorial species.

In insects adult size does not vary but animals do get older in the population. There is evidence that age affects individual mating success, both in territorial odonates^{9,12-13} and non-territorial odonates¹⁰⁻¹¹. Further, mating tactics, particularly in the Odonata, may be influenced by both size and age. As adult size is fixed, the effects of age and/or size can be distinguished from each other. In most odonates, adult life is short, and so these insects are useful to test theories of lifetime mating success. Furthermore, individuals can be marked and easily observed.

The aims of this study are to measure both female size in relation to fecundity, and the effects of size on male mating advantage in a non-territorial zygopteran.

MATERIAL AND METHODS

Census data

This study was conducted over two years from 13 November to 20 December 1989 and from 24 October to 29 November 1990 at a small pond within a nature reserve at Pelican Point, which is close to the city of Perth, Western Australia. The pond was surrounded to 80% by tall reeds (*Juncus kraussii*) while aquatic vegetation, primarily *Potamogeton pectinatus* and *Chara* spp., covered close to 90% of the pond's surface with only the middle of the pond as clear water. The bottom of the pond consisted of black silt with vegetation debris and plant stems and roots. Insects were netted around the pond and all of them were early emerged from larvae.

127 animals were captured and marked in 1989 and 124 in 1990. In 1989 marking was carried out over 10 days and in 1990 over 11 days. Head width and forewing lengths were measured and the wings marked with coloured enamel paints. Insects were then released. There was no observable effects of marking.

Censuses were made by walking around the perimeter of the pond every hour from 0900-1600 hrs. Notes were also made of mating and oviposition behaviour. Census data were sufficient to estimate daily sex ratios. Censusing was stopped when no marked animals could be found on three consecutive days. Observations were made over about six weeks in both years.

Size

Commonly the size of adult odonates differs between the beginning and end of the reproductive season¹⁴⁻¹⁵. To overcome the confounding problem of long term temporal variation I collected mating pairs and single males and females on the same day. Measures were taken of head width and wing length. Single females and females, which had already mated were

also collected before they had oviposited and others after oviposition. These females were brought to the laboratory and dissected where the number of eggs were counted.

Models

It was necessary to establish if males displayed territorial behaviour to perched males. Models were used as putative "residents" within areas commonly used as flight and perch locations of *X. erythroneurum*. The prediction was that if males were territorial they would attack the models; a behaviour commonly found in other odonates¹⁶.

Experiments, using model damselflies were performed between 1000 - 1430 hs, which is the most active time of the day for males and females. Mature males and females were caught with a hand net before the start of the experiments on each day. Either males or females were pinned through the thorax and the model was fixed to a small platform at the end of a thin 1 m stake. Once pinned, the models resembled, at least to the human observer, a naturally perching odonate.

Each model of either sex was controlled by a "sham model", which consisted of the perch alone. The sham model and experimental model were within 30 cm of each other. There were 80 replicates of both male (40) and female (40) models in the 10 day study.

A trial was considered valid when a male perched within 1 m of the model. Each trial was concluded after 5 min from the first sighting of the male. I recorded the frequency of two categories of behaviour; attack and non-attack. Non-attack behaviour was classified into investigatory behaviour and grasping. Males often attempted to copulate with the model. This behaviour was not treated differently from grasping.

RESULTS

Recapture rates

Recapture rates of marked animals were similar in the two years (28% in 1989 and 39% in 1990) ($\chi^2 = 1.44$; $df=1$; $P>0.05$). Males and females showed no significant difference in their recapture rate over the two years ($\chi^2 = 0.35$; $df=1$; $P>0.05$). Sexual maturity was defined as the first time an insect was observed to mate. Males and females reach sexual maturity at similar ages (Table 1).

The daily survival rate of males was about 80%, whereas that of females was about 70%. There was no difference between years ($\chi^2 = 0.66$; $df=1$; $P>0.05$) (Table 1). Mean life span, as measured by the duration of time each marked individual remained or re-visited the pond, was similar for both sexes (Table 1).

The daily sex ratio (male:female) of animals observed at the pond was always greater than one and at times as high as 9:1 (Figure 1). The mean sex ratio was 3.0 in 1989 and 2.0 in 1990. Sex ratio were especially male-biased during the early part of the day (Figure 2).

Mating behaviour

Males were observed flying during the period of survey, reaching a peak of activity between the hours of 1200 and 1300 (Figure 2). Females were present during the same period, and although not significantly different from the males, their peak flying time was slightly later than the males and their numbers declined during the afternoon, until all left after 1600 hs.

Table 1. Comparison of recaptured marked adults, sexual maturity, mean life span and daily survival rate of male and female of *X. erythroneurum* during 1989 and 1990.

	Male			Female		
	1989	1990	Ave	1989	1990	Ave
Recapture at least once	23	27	25	13	20	17
Sexual maturity(days) ¹	7.0±0.45 (n=9)	9.89±0.59 (n=9)	8	6.67±1.2 (n=4)	7.0±0.58 (n=7)	7
Mean life span (days) ²	6.12±1.3 (n=23)	7.19±1.02 (n=27)	6	4.6±1.4 (n=13)	4.95±0.99 (n=20)	5
Daily survival rate(%) ³	75	82	79	63	78	71

Note: 1. Sexual maturity animal defined as being sexually mature from the first time it was observed to mate.
 2. Adult lifespan was defined as the number of days between the date of marking and last sighting.
 3. Daily survival rate is calculated from exponential decay curve.

Table 2. Comparison of egg number in 3 categories of females: single females, paired females, and females completing oviposition. ANOVA of data mean log transformed to homogenize variance ($P>0.05$, Cochran's C-test).**a. mean number of egg (untransformed and transformed data)**

main effect	mean±se	number of eggs	
		mean (log)	n
single female	111±28	1.98	16
mating pair	345±28	2.52	16
finish laying eggs	11±5	0.64	8

b. analysis of variance

source	df	sum square	mean square	F	P
among group	2	18.85	9.42	73.95	0.0001
within group	37	4.72	0.13		
total	39	23.56			

c. multiple comparison among group (Scheffe F-test)

comparison	mean diff	F-test	P
single female vs mating pair	-0.53	8.93	<0.05
single female vs finish laying egg	1.34	37.71	<0.05
mating pair vs finish laying egg	1.88	73.63	<0.05

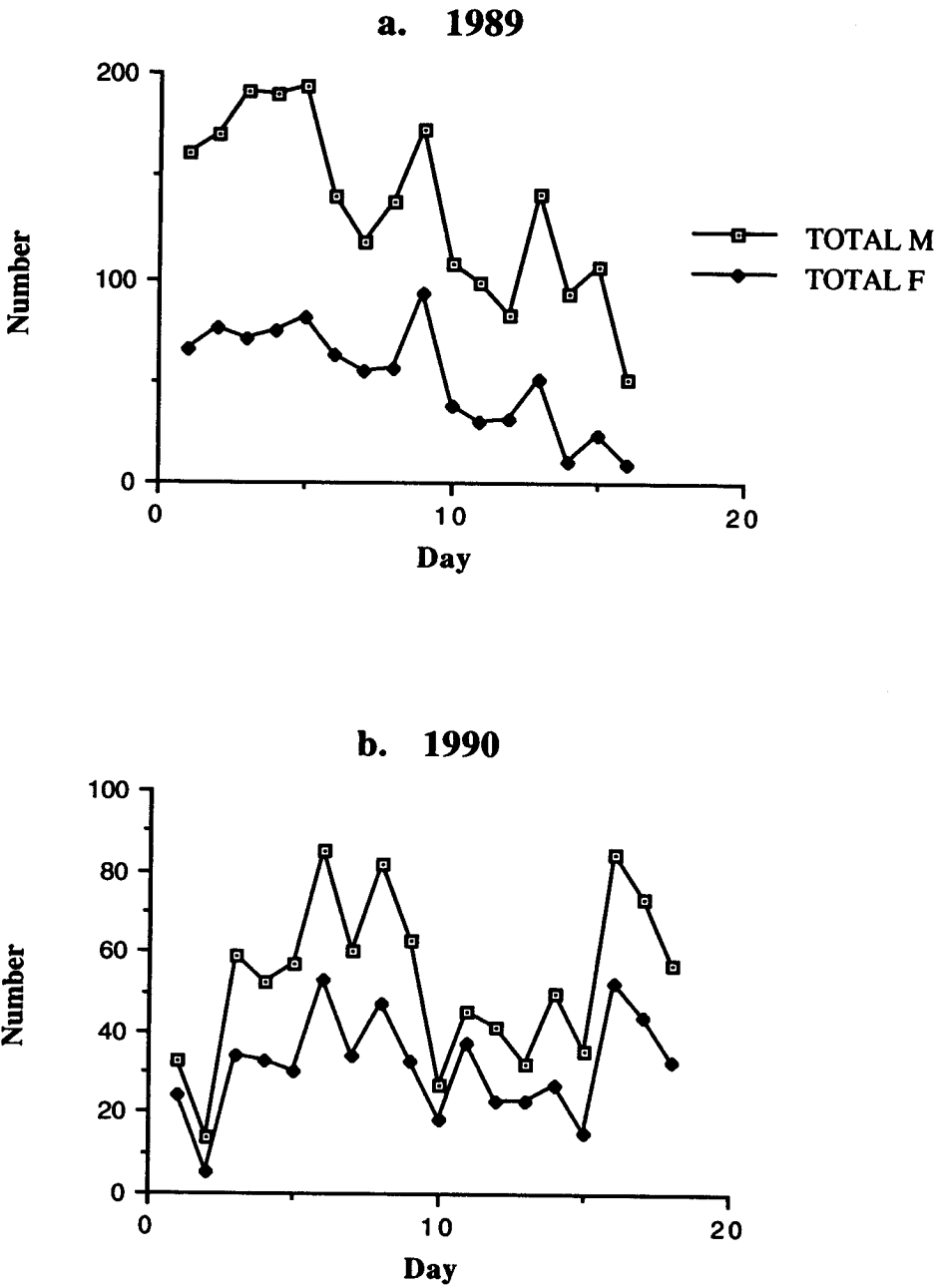


Fig.1. Number of males (M) and females (F) seen flying at the pond during each day of the 20 day study period. (a) 1989; (b) 1990.

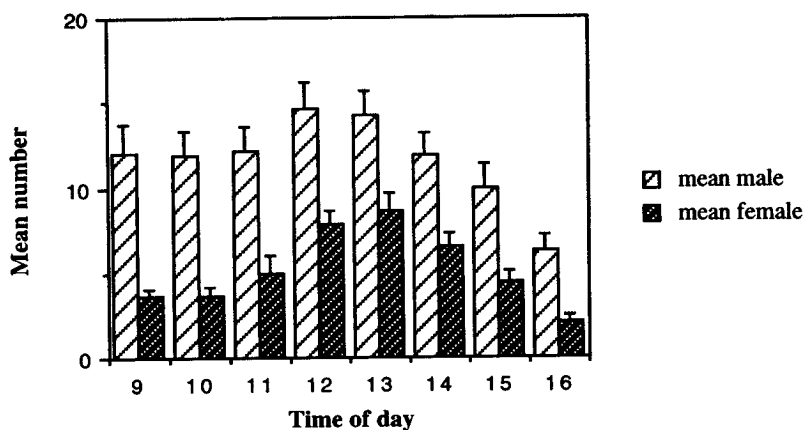


Fig.2. Counts of males and females seen during each hourly period over the two year study (mean \pm se).

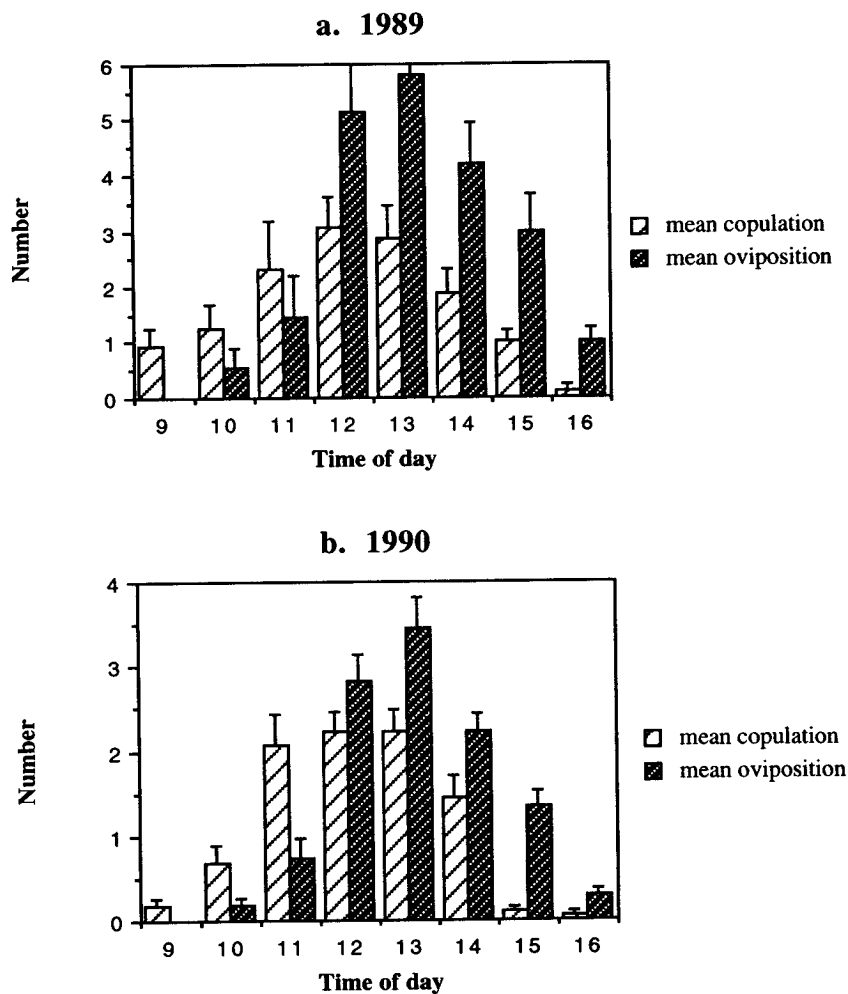


Fig.3. Number of copulations and ovipositions in each hour period. (a) 1989 and (b) 1990 (mean \pm se).

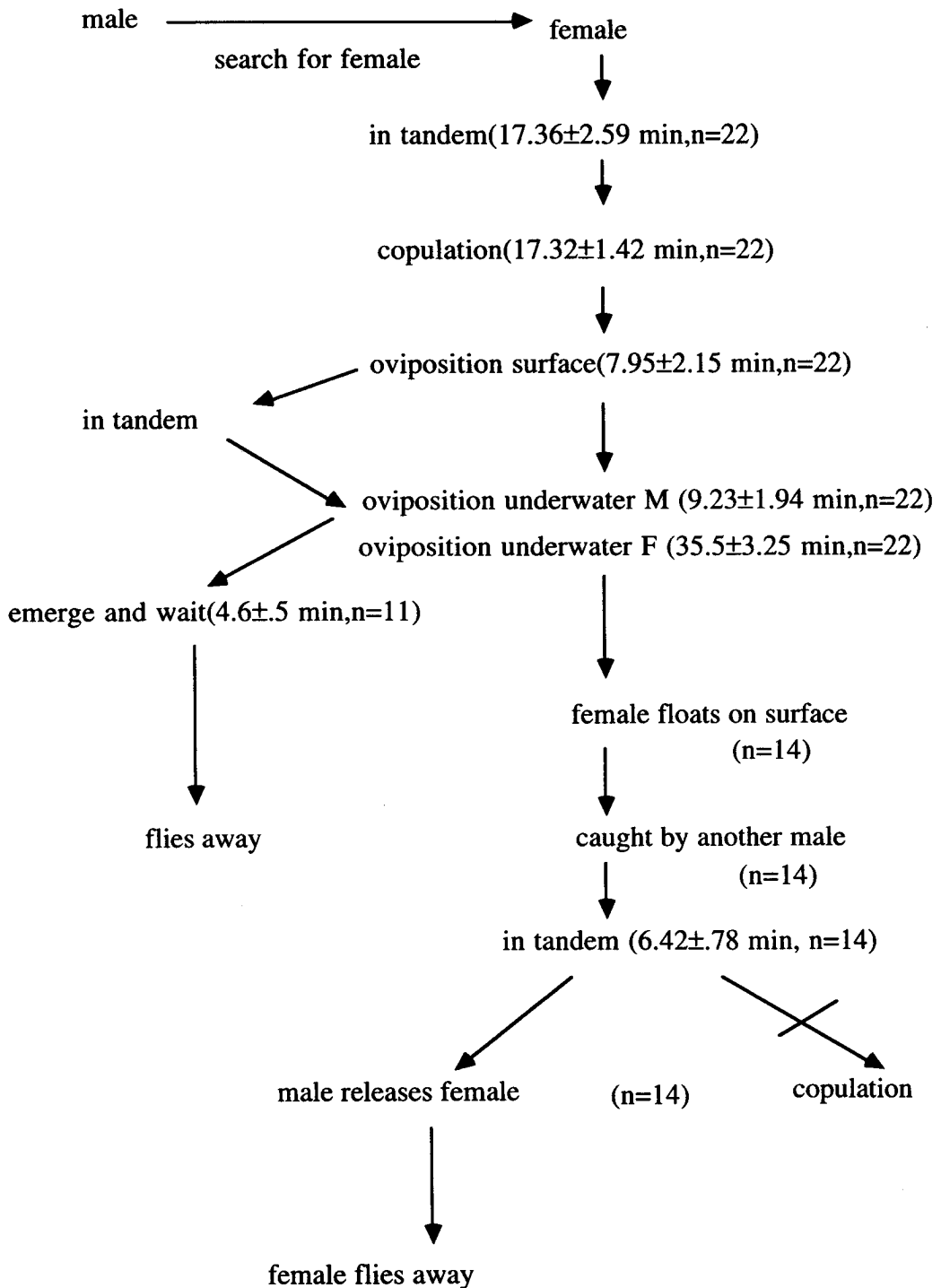


Fig.4. Mating behaviour sequence for *X. erythroneurum*. Values expressed as time (mean \pm se) and number of occurrences.

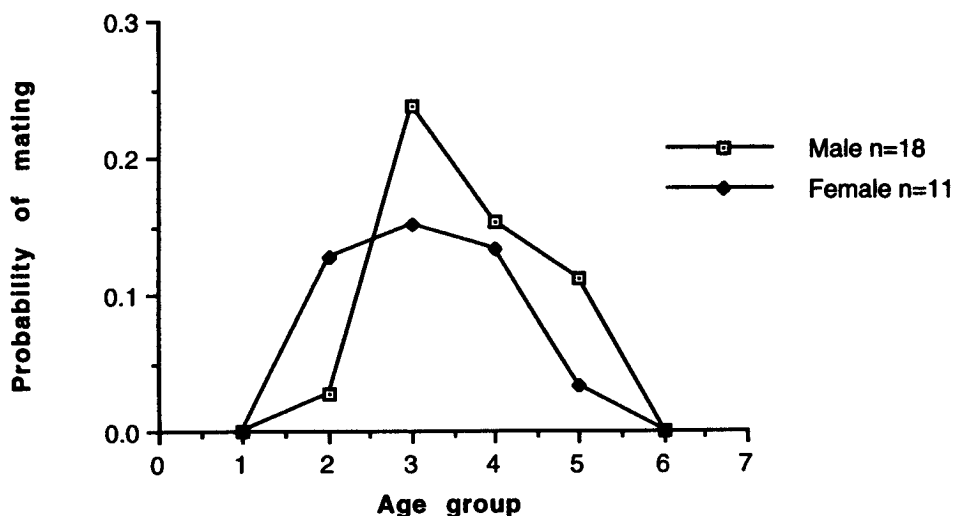


Fig.5. Effect of age on daily probability of obtaining a mate.

Age group is classified in 6 groups: age group 1=1-3, 2=4-7, 3=8-11, 4=12-15, 5=16-19, and 6=20-21 day old.

Most copulations occurred around midday (Figure 3), but some were observed in each hour between 0900 to 1600 hs. Oviposition events were not surprisingly slightly delayed to the observed times for copulation (Figure 3). Sixteen copulations were observed within 20 m of the margin of the pond but in all cases pairs came to the pond to lay eggs.

Male aggression and territoriality - experiments with models.

Searching behaviour by the male was distinctive. The male would make short flights between randomly selected perches. There was no evidence of site/perch preference. In the more than 800 hs of observation males were not seen interacting with other flying males, and interactions with perched males were very rare (<5).

When both male and female models were positioned at the edge of the pond, males demonstrated distinct pre-copulatory behaviours. Males would investigate the model and grasp its thorax (39/80 cases) before attempting to copulate. In all cases where males grasped the model they also curled their abdomen into the copulatory position. There was no significant difference between the number approaches and attempted copulations between male and female models ($t = 0.63$, $p = 0.53$, $n = 40$).

Cases where males showed aggressive behaviour, by approaching the model and the attacking it by "bumping" against it were rare (4/40 male models; 1/40 female models). In nature the only time this kind of behaviour was observed was when males approached paired insects that were either flying or perched in tandem (see below).

Courtship, Copulation and Oviposition.

Once the male located the receptive female copulation follows in a form typical for most odonates. The male would clasp the female by the prothorax with its anal appendages and within seconds the female curled its abdomen upwards, bringing the genitalia into contact with the male's accessory genitalia. This wheel position was held for approximately 17 min (Figure 4). Of the 22 observations made of this behaviour the female oviposited in all 22 cases (Figure 4).

After the male released the female he continued to guard her, remaining in the tandem position with the female unlocked from its genitalia. Tandem pairs flew close to the surface of the water, occasionally resting on reeds. Each pair, after a short flight, usually landed on the surface of the water some distance from the pond's edge. Although census of female oviposition sites was not undertaken, females appeared to prefer areas dense in aquatic submerged plants rather than open water. Initially, the female would lay her eggs on plants lying on the surface of the water, but after a short time she would crawl along the stems of aquatic plants, especially *Potamogeton pectinatus*, laying more eggs. This act took both pairs beneath the surface of the water where they remained, on average, for 9 min (Figure 4). The male would then emerge, often without the female. Males were observed to wait for the emerging female, flying low over the oviposition site or resting nearby for on average 5 min (Figure 4). During these observations 11 males simply disappeared and may have remained below the surface for longer than the time given for observation (up to 1 hr), or they may have been eaten by predators. In 14 cases the female was left alone to complete oviposition. The longest time any female was observed to remain beneath the water was 70 min (mean time for submersion was 35.5 ± 3.25 (SE) min, $n = 22$).

After completing oviposition underwater females would then return to the surface where males, flying over the oviposition site or resting on the tall reeds nearby, attempted to copulate with the surfacing females (14 of 22 cases). In all cases the female was caught by the male (Figure 4). Even if the female was trapped on the water surface, males still attempted to clasp her in the tandem position. Although males were able to retain females in the tandem position they never achieved the wheel position and males gave up after several minutes (Figure 4), eventually permitting females to fly away.

Males were observed harassing both tandem pairs ($n=12$) and pairs in the wheel position ($n=9$). This behaviour included strikes by the wings and abdomen and this occasionally resulted in wing damage to the attacking male ($n=3$).

Mating success

Of the 95 males marked in 1989, and the 53 in 1990, only 23 returned to the pond in 1989 and 27 in 1990. Of these returning insects 9 males obtained a mate in 1989 and 9 in 1990. In 1989, 32 females were marked and 69 in 1990 and again 13 returned in 1989 and 20 in 1990. In the first year, 4 females were observed mating and in 1990 there were 7. Observed matings for individual marked (returned) males and females varied from zero (no matings) to 4 (multiple matings). That an animal is no longer at the pond may not mean it is dead, however a number of workers have made this assumption in calculating life history parameters (e.g. Banks and Thompson¹⁰).

Considering only animals that reached sexual maturity, and those that only mated at the focal pond, the variance in mating success of males (0.89; $n=18$) was not significantly different from that of females (1.06 ; $n=11$) ($F=1.19$, $P>0.05$).

Body size and mating success

Head width and wing length of marked insects did not differ significantly between mated and non-mated animals (head width, male: $F = 1.19$, $P = 0.28$, $df = 1$; female $F = 0.86$, $P = 0.36$, $df = 1$; wing length, male $F = 3.58$, $P = 0.06$, $df = 1$; female $F = 0.301$, $P = 0.58$, $df = 1$; ANOVA).

Comparing only males and females that had reached sexual maturity, (> 5 days for females; > 6 days for males) there was no relationship between size and mating success for

either sex (head width, male: $F = 0.43$, $P = 0.52$, $df = 1$; female $F = 0.10$; $P = 0.76$, $df = 1$; wing length, male $F = 0.20$, $P = 0.66$, $df = 1$; female $F = 1.35$, $P = 0.28$, $df = 1$; ANOVA). Body size did not affect survival of either males or females (head width, male: $F = 0.03$, $P = 0.85$, $df = 1$; female $F = 0.30$, $P = 0.58$, $df = 1$; wing length, male $F = 1.89$, $P = 0.17$, $df = 1$; female $F = 0.53$, $P = 0.47$, $df = 1$; ANOVA).

Trials were conducted over two years where size differences were observed between years in each of the classes. Such year effects are independent of the hypothesis under question as insects would be unable to mate with cohorts from different years. In order to confirm the lack of relationship between size and mating success the data set was increased by examining all insects from two collecting sites on one day (mated pairs 16, non-mating males 20 and females 16). There was still no significant difference in head width and wing length between mated and non-mated animals (Scheffe F-test; head width: male, $F = 0.28$, $p = 0.6$; female $F = 2.93$, $p = 0.1$; wing length: male $F = 0.09$, $p = 0.76$; female $F = 0.14$, $p = 0.71$).

Mating success and the effects of age

Males and females of intermediate age (7-9 days) obtained the most mates (Figure 5). The youngest animal to obtain a mate were 5 days and the oldest 19 days.

Clearly age should be related to life-time mating opportunity: the more opportunities an adult has to mate the more times it will be observed mating. Confirming this prediction, longevity, as estimated by the number of days at the pond and the number of matings, was strongly correlated in males and females (Spearman rank correlation; male: $r = 0.50$, $P=0.02$, $n=18$; female: $r = 0.60$, $P=0.02$, $n=11$). Connected to this prediction was that males and females visiting the breeding area more frequently obtained more mates than those making single visits (Mann Whitney Test; male $P = 0.0001$; female $P = 0.01$).

I was unable to observe single females throughout a whole day. However, if females were to mate more than once they would carry their full compliment of eggs. Egg number in the reproductive tract of mating females were compared with those that had just completed ovipositing. Females lay almost all of their eggs at oviposition (Table 2). As single, unmated females had fewer eggs than pre-oviposition mated females it is highly suggestive that egg replenishment takes longer than one day and that females do not mate more than once per day.

Size and fecundity of females

Although size is usually a good predictor of fecundity in insects, in *X. erythroneurum* there was no significant correlation between body size and number of eggs in pre-oviposition mated females (Spearman rank correlation; $r=0.27$; $P=0.13$; $n=32$; head width; and $r=0.09$; $P=0.64$; $n=32$; wing length).

DISCUSSION

Sex ratios

There are clearly more males at the lake at any one time than there are females (Figure 1) and females only mate once during any one day. Given such a bias in the operational sex ratio males should compete for relatively scarce females and one expression of this competition should be the early arrival of males to the pond before females, a common feature of other odonates (c.f. Alcock¹⁷). In such cases, where early arrival indicated male-male competition, the behaviour was usually associated with males establishing themselves at optimal female

resources. This argument cannot be applied to *X. erythroneurum* where resource defence has not been demonstrated.

Why then the disjunct arrival times of males and females at the pond? Although competition for females may be far weaker than in Anisoptera such as *Orthetrum caledonicum*¹⁷, nevertheless competition may still occur, not through overt aggression but more simply that males, present at the pond at the time of female arrival, will have first chance of intercepting and mating with females. Further, it has been demonstrated elsewhere (Watanasit Manuscript submitted) that sperm displacement occurs in this species. And so early mating males will be assured of unmated females which will have sufficient time to oviposit.

Variation in mating success - Inter-sexual variation.

By using a focal pond in an area where alternative mating sites were relatively abundant any absolute measure of individual mating success must be conservative and measures of adult longevity impossible to achieve; the best expectation is the length of time any one individual is resident at one pond. Data from the focal pond showed that about 90% of adult males and female *X. erythroneurum* did not mate at all.

The highest number of matings by one individual, returning to the same pond, was four, and the variance in mating success of both males and females at this pond was equal. Predictably, variation in mating success will relate to the relative investment in the offspring by each sex¹⁸, and in many odonates, where males actively defend territories that are associated with female oviposition sites, a high variation in male mating success, compared to female, should be expected. In *X. erythroneurum* we found no evidence of either territorial behaviour or male aggression to other single males; the sexes met close to the pond and both sexes flew in tandem to a suitable egg laying site. The absence of differences in the mating success of either sex was also found by Hafernik and Garrison¹⁹ in the damselfly *Ischnura gemina*.

For many odonates male investment in courtship is high, with energy expended in the maintenance of territories. Displays between rival males often involves flight displays accompanied by displays of brightly coloured body parts and it is assured that sexual dimorphism often results from strong selection on these male displays. Such conspicuousness has its costs through risks of predation where brightly coloured males are subject to higher predation risks than females²⁰⁻²⁵. The selective advantages of risk taking by displaying males must come from increased opportunities to inseminate females²⁶ and so such risks should lead to a greater variation in mating success for males than for females. Obtaining evidence that demonstrates selection on male courtship through risks of predation alone is extremely difficult²⁷, and where events are episodic, recording the event in nature is often impossible. Experience of predation at the pond was no exception but there was some indication that males were more subject to predation on the wing than females (an observation that needs to be viewed with some caution considering the skewed sex ratio).

Undoubtedly the operational sex ratio is dependent on the readiness of each sex to mate. When sperm replenishment is more rapid than egg replacement, more males should be at the pond, ready to mate, than females. And so the operational sex ratio may be linked to the length of time each sex takes to reach sexual activity. Most field experimental data on damselfly mating systems show that males are able to mate multiply within one day (e.g. Banks and Thompson¹⁰; Fincke¹¹) but it was not possible to confirm this with *X. erythroneurum*; although marked males returned to the pond more than once these males were not observed to mate.

Females invest more time in their egg production and as a consequence, females only visited the pond infrequently to mate and oviposit, remaining around the pond until the late afternoon. Thus, based on evidence of the operational sex ratio, 3 in 1989 and 2 in 1990, variation in mating success should still be higher in males.

Individual mating success - Size and age

Larval success should be reflected in the size of the final instar and should then be translated to reproductive success through the emerging adult's competitive ability (males), fecundity (females), its survivorship and longevity. This study provides evidence for individual variation in mating success (0-4 matings). Given serial monogamy in this species and that females mate with the first male they encounter, size will be under weak selection through female choice and, consistent with this, we found adult body size had no effect on mating success. But if female choice, based on size, was present, perhaps at a more subtle level, evidence from the sampling process used may have been obscured by the extremely small size variation encountered in the natural population. For example the coefficient of variation (CV) found for males collected during January 1990 was 6.2% for measurements of head width and 2.9% for wing length.

A second explanation as to why size had no demonstrable effect on mating success is that both male and female *X. erythroneurum* fly when they are in tandem. In species where females are weak fliers, or where they do not fly at all, size may be advantageous for males in carrying passive females in flight. Banks and Thompson¹⁰ point out that unlike the dung fly (*Scatophaga stercoraria*), where the male carries the passive female²⁸, in damselflies male size advantage will be unlikely to have any selective advantage for this purpose. Further, Marden and Waage²⁹ found that even in a highly territorial damselfly body size was not the key factor but rather the level of fat reserves.

Males actively seeking females at any one time will vary in age. We found that "middle-aged" adults, 7-9 days old, were most likely to obtain mates. Young adults do not obtain mates because they are not sexually mature and older animals were less likely to obtain mates because of declining physiology and physical damage associated with aging^{10,12}. The wings of older males and females of *X. erythroneurum* were often tattered, perhaps due to physical encounters during harassment at copulation and oviposition.

Do females mate more than once in a day?

Females were never observed to mate more than once within a single day at the pond. But evidence for low frequency of mating within a single day was more clearly derived from the presence or absence of eggs in captured females. Counts of eggs show that females lay almost all their eggs in a single oviposition. Females captured alone had fewer eggs than females captured in copulation, suggesting that replenishment of eggs takes time. As egg replenishment takes longer than one day it is highly unlikely that females are able to mate more than once in a single day.

Males appeared unable to distinguish between mated and unmated females. On the 14 occasions where males encountered post-copula females, each time the female rejected the male after several minutes in tandem. Of the 22 observations on copulating pairs no intruding males were successful in breaking up a tandem pair and so it was not possible to establish whether females, once in copula could remate with other males. However, given the strong selection on retaining the tandem position after copulation (14 from 22) it is highly likely that if females were released by the male before oviposition, she would mate with a second male.

ACKNOWLEDGEMENTS

I would like to thank Dr. Winston Bailey, Zoology Department, The University of Western Australia, for his comment. I also thank to Dr. Louis Leble, CSIRO, Division of Wildlife & Ecology, Canberra, Australia, for his encouragement and discussion the project. I am grateful to the International Development Programme (IDP), Australia, for supporting and funding this project.

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บทคัดย่อ

ทำการศึกษาพฤติกรรมแมลงปอเข็ม *Xanthagrion erythroneurum* (Zygoptera: Coenagrionidae) บริเวณสระน้ำใกล้เมืองเพิร์ท รัฐออสเตรเลียตะวันตก ประเทศออสเตรเลียในช่วง 2 ปี ระหว่างปี 2532-2533 ในแต่ละปีได้ทำการสำรวจแมลงปอเข็มที่ทำเครื่องหมายไว้ที่ปีกก่อนแล้ว การสำรวจกระทำทุกวันตั้งแต่เวลา 8.00 - 16.00 น. เป็นเวลา 6 สัปดาห์ของแต่ละปี ทำการบันทึกพฤติกรรมการผสมพันธุ์และการวางไข่ของแมลงปอเข็มแต่ละตัว (individuals) นอกจากนั้นได้ทำการทดสอบพฤติกรรมระหว่างตัวผู้ด้วยกันโดยใช้หุ่นจำลอง (model) ซึ่งมีทั้งตัวผู้และตัวเมีย

ผลการศึกษาพบว่าอัตราส่วนระหว่างเพศ (sex ratio) ของแมลงปอเข็มพบเพศผู้มากกว่าเพศเมีย โดยตัวผู้จะมาถึงสระน้ำก่อนตัวเมีย หลังจากลอกคราบเป็นตัวเต็มวัย ทั้งสองเพศสามารถถึงวัยสืบพันธุ์ (sexual maturity) ภายใน 8 วัน อัตราการอยู่รอดในแต่ละวัน (daily survival rate) ประมาณ 80% และ 70% สำหรับตัวผู้และตัวเมียตามลำดับ โดยคำนวณจากจำนวนวันที่ตัวผู้และตัวเมียกลับมายังสระที่ศึกษา

ตัวผู้ไม่มีพฤติกรรมก้าวร้าว (agonistic behaviour) ต่อตัวผู้ตัวอื่นที่บินผ่าน ต่อตัวผู้ที่เกาะอยู่รอบสระ หรือต่อหุ่นจำลองทั้งสองเพศ ซึ่งแสดงให้เห็นว่า *X. erythroneurum* ไม่มีพฤติกรรมของการครอบครองอาณาเขต (territorial behaviour)

พฤติกรรมการผสมพันธุ์ (mating behaviour) ตัวผู้จะคอยจับตัวเมียที่เกาะอยู่ตามพืชน้ำบริเวณสระน้ำและตัวเมียที่บินผ่านมา เมื่อตัวผู้จับตัวเมียได้ก็จะอยู่เป็นคู่ (tandem) จากนั้นตัวเมียจะโค้งตัวเข้าหาตัวผู้ลักษณะเป็นวงกลม (wheel position) ซึ่งเป็นพฤติกรรมโดยปกติของแมลงในกลุ่มนี้ การวางไข่จะเกิดขึ้นหลังการผสมพันธุ์ พบว่าตัวผู้ปกป้องตัวเมียขณะที่ตัวเมียวางไข่ได้ น้ำ โดยบินรอบๆ บริเวณที่ตัวเมียวางไข่อยู่ ตัวเมียวางไข่ใต้น้ำใช้เวลาเฉลี่ยประมาณ 35 นาที เมื่อตัวเมียเสร็จสิ้นการวางไข่โผล่จากผิวน้ำ ตัวผู้อื่นพยายามที่จะผสมกับตัวเมีย โดยอยู่ในลักษณะเป็นคู่หลายนาที เมื่อตัวเมียไม่ยอมให้ผสมก็จะปล่อยตัวเมียให้เป็นอิสระ จากการสังเกตไม่พบตัวเมียผสมอีกเลยในวันนั้น

ถึงแม้ว่าอายุ มีผลต่อการประสบความสำเร็จในการผสมพันธุ์ (mating success) แต่ขนาดของแมลงตัวเต็มวัย (ความกว้างของหัวและความยาวของปีก) ของตัวผู้และตัวเมียไม่มีผลต่อการประสบความสำเร็จในการผสมพันธุ์ อายุของตัวผู้และตัวเมียประมาณ 7 วัน มีโอกาสในการสืบพันธุ์สูงสุด